



Hiding in the background: community-level patterns in invertebrate herbivory across the tundra biome

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Abstract

Invertebrate herbivores depend on external temperature for growth and metabolism. Continued warming in tundra ecosystems is proposed to result in increased invertebrate herbivory. However, empirical data about how current levels of invertebrate herbivory vary across the Arctic is limited and generally restricted to a single host plant or a small group of species, so predicting future change remains challenging. We investigated large-scale patterns of invertebrate herbivory across the tundra biome at the community level and explored how these patterns are related to long-term climatic conditions and year-of-sampling weather, habitat characteristics, and aboveground biomass production. Utilizing a standardized protocol, we collected samples from 92 plots nested within 20 tundra sites during summer 2015. We estimated the community-weighted biomass lost based on the total leaf area consumed by invertebrates for the most common plant species within each plot. Overall, invertebrate herbivory was prevalent at low intensities across the tundra, with estimates averaging 0.94% and ranging between 0.02 and 5.69% of plant biomass. Our results suggest that mid-summer temperature influences the intensity of invertebrate herbivory at the community level, consistent with the hypothesis that climate warming should increase plant losses to invertebrates in the tundra. However, most of the observed variation in herbivory was associated with other site level characteristics, indicating that other local ecological factors also play an important role. More details about the local drivers of invertebrate herbivory are necessary to predict the consequences for rapidly changing tundra ecosystems.

Keywords Background herbivory · Biomass loss · Climate change · Community-weighted average · Invertebrate · Insects · Tundra

Introduction

Invertebrate herbivores can have strong effects on the structure and function of Arctic ecosystems. Most studies of invertebrate herbivory in high-latitude systems have focused on outbreak events, when herbivores consume massive amounts of plant biomass over a short time period. Outbreaks have most frequently been reported for boreal forests

and the forest-tundra ecotone (Jepsen et al. 2013; Karlsen et al. 2013; Kaukonen et al. 2013) whereas few have been described in true tundra systems (Post and Pedersen 2008; Lund et al. 2017). In contrast, under non-outbreak densities, invertebrates are responsible for low but chronic biomass removal, referred to as background herbivory (Kozlov and Zvereva 2017). At these low densities the immediate effects of invertebrates appear minimal (Kotaniemi and Rosenthal 2000), but the longer-term nature of background herbivory may have prolonged effects on plant growth (Zvereva et al. 2012), community interactions (Barrio et al. 2013), and nutrient fluxes (Metcalf et al. 2016). The current understanding of the patterns of background invertebrate herbivory in tundra environments is based on only a few studies that focused on either a single host plant species (*Betula*

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glandulosa-nana complex, Barrio et al. 2017) or on specific growth forms (shrubs, Kozlov et al. 2015a). No studies have assessed patterns of invertebrate background herbivory at the community level across the tundra biome.

The interaction between invertebrate herbivores and plants in tundra ecosystems occurs under environmental conditions characterized by cold temperatures, a short growing season, and precipitation that falls mostly as snow (Strathdee and Bale 1998). Current trends associated with rapid climate change at high latitudes indicate that the tundra biome will continue to experience increased temperature and altered precipitation regimes, as well as a longer growing season (Post et al. 2009; IPCC 2013; Overland et al. 2017). Invertebrate ecophysiology strongly depends on temperature, so even moderate increases in temperature have the potential to alter the duration of the life cycles (or parts of them) of invertebrate herbivores, increase their densities and activity (Asmus et al. 2018), or alter their distribution ranges or those of their competitors (Hodkinson and Bird 1998; Bale et al. 2002; Bolduc et al. 2013). For example, higher summer temperatures can increase the intensity of herbivory (Birkemoe et al. 2016), create phenological mismatches between specialist herbivores and plant species (Kharouba et al. 2015) or alternatively, induce stronger phenological matches between plants and herbivores (Jepsen et al. 2011; Pureswaran et al. 2019), and/or alter herbivore feeding choices (Barrio et al. 2016a), although these patterns are far from being general in either space or time (Kozlov and Zvereva 2015; Zvereva et al. 2016; Kozlov et al. 2017). Moreover, changes in precipitation could affect the amount of damage caused by invertebrate herbivores indirectly, through their influence on leaf traits, such as leaf toughness (based on the structural materials that make up the leaf) or leaf chemistry. Stress due to dry conditions can either increase the toughness of leaves, thus decreasing their palatability for invertebrate herbivores (Onoda et al. 2011) or induce plants to decrease the production of herbivore defense chemicals, resulting in an increase in the palatability of leaf tissues (Berg et al. 2008). Kozlov et al. (2015b) found that precipitation contributed to latitudinal patterns observed in invertebrate herbivory, such that increased precipitation resulted in higher levels of invertebrate-caused defoliation. With the potential for so many different responses to climate change, it is essential to document the existing patterns of invertebrate herbivory and to explore the drivers behind these patterns in order to predict future changes.

The level of herbivory on plants can also be driven by local site characteristics, such as habitat type, productivity, or plant community composition. Herbivory is generally lower in more diverse plant communities, but this varies with the host specificity of insects, and plant species composition may be more important than species richness per se (Jactel and Brockerhoff 2007). For example, different growth

forms or functional groups of plants differ in their palatability and responses to herbivory (Turcotte et al. 2014). In general, deciduous shrubs are more palatable than evergreen shrubs (MacLean Jr. and Jensen 1985; Turcotte et al. 2014), and shrubs, due to plant apparency, tend to be consumed more than herbaceous plants (Turcotte et al. 2014). Graminoid species are often less palatable due to lower nutritional content and stronger physical defenses (Tscharntke and Greiler 1995). Thus, local and site level factors influencing variation in herbivory need to be considered in combination with climate drivers.

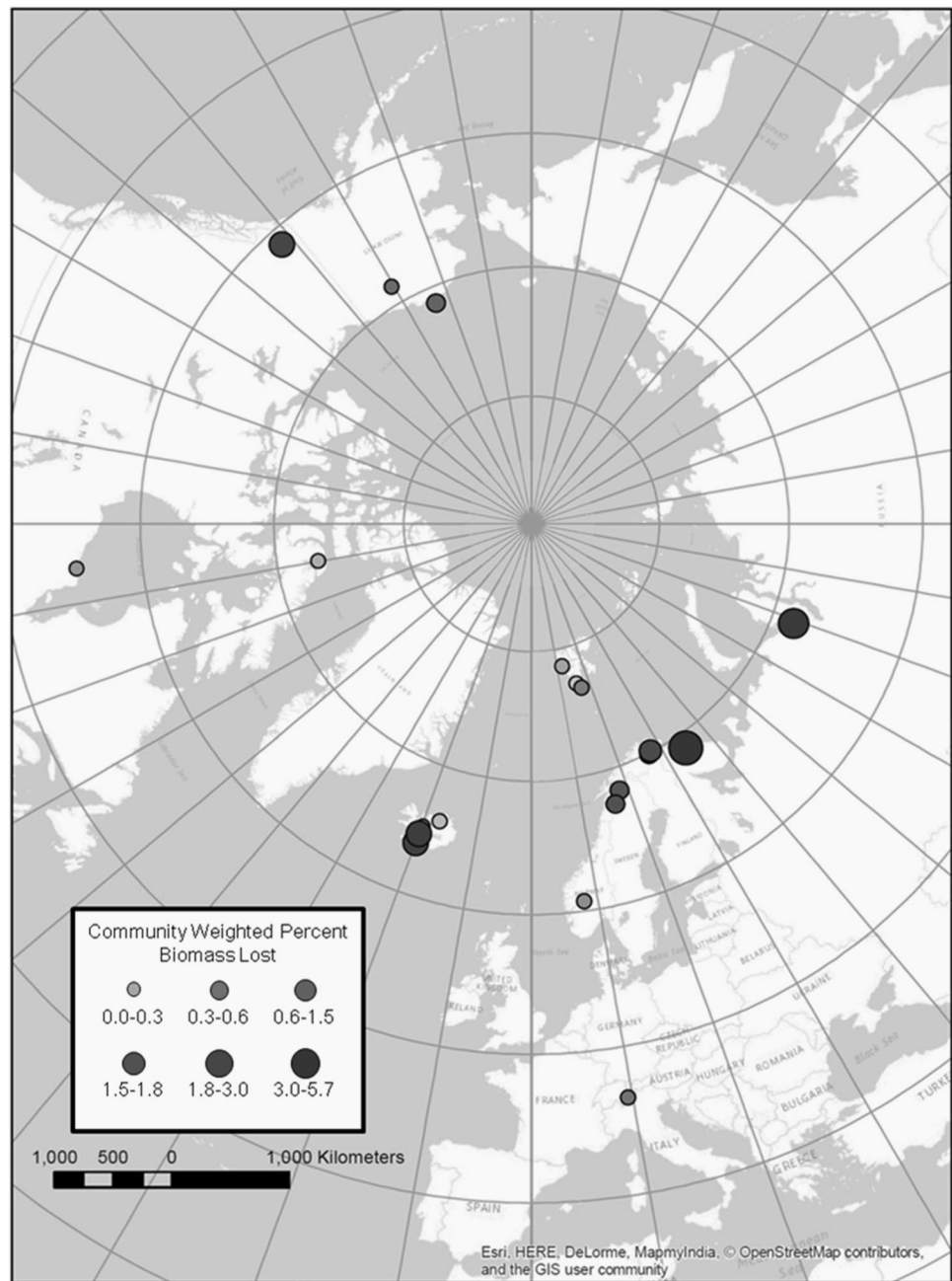
We assessed invertebrate herbivory within vascular plant communities across the tundra biome to investigate the role of climatic drivers, specifically temperature and precipitation, habitat, and aboveground plant biomass, in explaining the variation in plant losses to invertebrate herbivores. We predicted that higher levels of invertebrate herbivory would be associated with sites experiencing higher summer temperatures and higher precipitation, and would vary across habitats with different aboveground biomass availability, such that sites with more plant biomass will experience higher levels of herbivory (Bonser and Reader 1995). We also assessed the hypothesis that different plant functional groups (deciduous shrub, evergreen shrub, graminoid, herbs) experience different levels of herbivory due to differences in palatability, such that deciduous shrubs would have more damage than evergreen shrubs, shrubs would have more damage than herbaceous plants, and that herbs would have more damage than graminoids. To do this we examined invertebrate herbivory at the species level for 42 vascular plant species grouped into broad functional groups. To our knowledge, this is the first survey of community level invertebrate herbivory in the tundra. Our coordinated study may provide a framework for future global monitoring efforts of invertebrate herbivory in other ecosystems too.

Methods

Study design

This study was conducted during the summer of 2015 and involved researchers working at 20 Arctic/alpine tundra sites in the Northern Hemisphere (Fig. 1). In order to ensure consistent data collection, we adopted a common protocol designed by the Herbivory Network (Barrio et al. 2016b; Online Resource 1) that provided a simple, hierarchical design for sampling individual plants and plots within each study site. The protocol was distributed to members of the Herbivory Network who generally selected locations associated with their own long-term research efforts; these sites are described in more detail in Rheubottom (2018). Sites spanned high-latitude tundra ecosystems ranging from 55.24

Fig. 1 Community-weighted biomass lost (CWBL) to invertebrate herbivores at each of the 20 tundra sites. Size and shade of dots indicate intensity of herbivory, grouped into 6 bins. Audkuluheidi (Iceland) and Ailigas (Finland) (see Table 1) are covered by nearby sites, and belong in the 0.0–0.3 bin and 0.3–0.6 CWBL bins, respectively



to 78.60°N and one alpine site in the Swiss Alps (Val Bercla 46.47°N).

A study site was broadly defined as an area of 0.25–25 km² where sampling was conducted. At each site, the dominant habitat type was identified, avoiding areas influenced by extremes in moisture, soil chemistry, or disturbances, so that study sites would represent a variety of habitats characteristic of the tundra biome (Table 1). Habitat types were determined based on the broader habitat categories defined in the Circumpolar Arctic Vegetation Map (CAVM; Walker et al. 2005), or were classified as alpine tundra. Latnjajaure was included in the erect-shrub tundra category based on a

similar definition from Virtanen et al. (2016). Overall, a total of 6 habitat types were considered (Table 1).

At each site, five plots (20 × 20 m) were established at least 100 m apart. Three focal species of vascular plants were identified in each plot based on their overall contribution to the community-wide foliar biomass, with the exception of Toolik Lake where five focal species were sampled (Table 1). Consequently, the focal species were plot-specific and could differ between plots within the same study site. In total, 42 focal species were sampled across all sites, including 13 graminoids, 9 deciduous shrubs, 8 evergreen shrubs, and 12 herbs (Table 2).

Table 1 Description of the 20 study sites across the tundra biome: name abbreviation in capital letters and coordinates in decimal degrees are shown in brackets; sampling date(s) in 2015, elevation, dominant habitat type (broad habitat types as defined by Walker et al. (2005); more specific CAVM sub-categories are included in brackets when possible), number of plots sampled, identity of the focal species (and the number of plots in which each focal species was found at each site), and climate variables: long-term average (1990–2015) and 2015 July temperature and precipitation (CRU data from Harris et al. (2014) for the nearest grid cell with complete information)

Study site	Region	Sampling date(s)	Elevation (m a.s.l.)	Habitat type	Number of plots	Focal Species (number of plots present)	Mean July temperature (1990–2015) (°C)	Mean July precipitation (1990–2015) (mm)	Mean July temperature (2015) (°C)	July precipitation (2015) (mm)
Burntpoint Creek BURN (55.24, – 84.32)	Canada	June 25	7–8	Wetlands (W2)	4	<i>Carex aquatilis</i> (4), <i>Trichophorum cespitosum</i> (4), <i>Andromeda polifolia</i> (4)	14.8	85.3	14.6	80.0
Bylot Island BYLOT (73.15, – 79.99)	Canada	July 16	44–102	Graminoid (G2)	5	<i>Cassiope tetragona</i> (4), <i>Salix arctica</i> (5), <i>Arctagrostis latifolia</i> (4), <i>Oxyria digyna</i> (1), <i>Papaver radicum</i> (1)	5.6	36.6	7.5	18.0
Pika Camp PIKA (61.22, – 138.27)	Canada	July 27	1637–1774	Prostrate-shrub (P1)	5	<i>Dryas octopetala</i> (5), <i>Salix arctica</i> (4), <i>Carex bigelowii</i> (5), <i>Salix reticulata</i> (1)	10.3	58.0	10.5	80.4
Ailigas AILIG (69.89, 27.07)	Finland	Aug 11–13	339–346	Erect-shrub (S1)	5	<i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>Vaccinium vitis-idaea</i> (5)	12.7	77.8	10.5	32.7
Njallavaara NJAL (70.04, 27.60)	Finland	Aug 20–21	266–281	Erect-shrub (S1)	5	<i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>V. vitis-idaea</i> (5)	12.4	70.9	10.3	27.2
Audkuluheidi AUDK (65.13, – 19.67)	Iceland	Aug 4	479–498	Prostrate-shrub (P1)	5	<i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>Silene acaulis</i> (2), <i>Vaccinium uliginosum</i> (3)	10.2	48.5	8.4	40.5

Table 1 (continued)

Study site	Region	Sampling date(s)	Elevation (m a.s.l.)	Habitat type	Number of plots	Focal Species (number of plots present)	Mean July temperature (1990–2015) (°C)	Mean July precipitation (1990–2015) (mm)	Mean July temperature (2015) (°C)	July precipitation (2015) (mm)
Fjallabak FJAL (63.83, – 19.91)	Iceland	Aug 29	648–657	Barren (B1)	5	<i>Salix herbacea</i> (5), <i>Armeria maritima</i> (4), <i>Cerastium alpinum</i> (1), <i>Salix arctica</i> (2), <i>O. digyna</i> (2)	9.9	94.5	8.5	57.4
Skálpanes SKAL (64.52, – 19.91)	Iceland	Aug 15	622–641	Barren (B1)	5	<i>Salix herbacea</i> (5), <i>Silene acaulis</i> (5), <i>Juncus trifidus</i> (2), <i>Armeria maritima</i> (2), <i>Luzula spicata</i> (1)	8.9	66.6	7.2	49.0
Theistareykir THEIS (65.9, – 17.08)	Iceland	Aug 2	326–341	Prostrate-shrub (P1)	5	<i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>Calluna vulgaris</i> (5)	10.3	54.8	7.9	76.7
Hol HOL (60.70, 7.94)	Norway	July 17–20	1092–1147	Erect-shrub (S2)	4	<i>Betula nana</i> (4), <i>Vaccinium myrtillus</i> (4), <i>V. uliginosum</i> (1), <i>Avenella flexuosa</i> (3)	11.9	80.9	10.7	74.9
Erkuta ERKUT (68.23, 69.15)	Russia	Aug 1–3	18	Wetlands (W3)	5	<i>Betula nana</i> (5), <i>V. vitis-idea</i> (5), <i>Carex</i> sp. (5)	12.9	41.0	11.2	60.1
Murmansk MURM (68.87, 34.54)	Russia	Aug 11	246–265	Erect-shrub (S1)	5	<i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>V. myrtillus</i> (5)	13.0	69.3	10.3	46.6
Bogstranda BOGST (77.02, 15.75)	Svalbard	July 18	20–37	Prostrate-shrub (P1)	5	<i>Salix polaris</i> (5), <i>Saxifraga oppositifolia</i> (5), <i>Festuca rubra</i> (5)	4.4	46.0	4.6	32.5

Table 1 (continued)

Study site	Region	Sampling date(s)	Elevation (m a.s.l.)	Habitat type	Number of plots	Focal Species (number of plots present)	Mean July temperature (1990–2015) (°C)	Mean July precipitation (1990–2015) (mm)	Mean July temperature (2015) (°C)	July precipitation (2015) (mm)
Kaffiøyra KAFFI (78.60, 12.24)	Svalbard	July 14	27–31	Prostrate-shrub (P1)	5	<i>D. octopetala</i> (3), <i>Salix polaris</i> (5), <i>Silene acaulis</i> (5), <i>Saxifraga oppositifolia</i> (1), <i>Bistorta vivipara</i> (1)	2.9	53.1	3.6	56.0
Kikutodden KIKUT (76.61, 16.96)	Svalbard	July 17	11–18	Barren (B1)	3	<i>Luzula confusa</i> (3), <i>Cochlearia groenlandica</i> (1), <i>Poa arctica</i> (1), <i>Salix polaris</i> (1), <i>Saxifraga hyperborea</i> (1), <i>Cerastium arcticum</i> (2)	4.3	48.2	4.3	35.0
Latnjajaure LATN (68.21, 18.29)	Sweden	Aug 4	1000	Erect-shrub (Low Arctic dwarf birch tundra ^a)	1	<i>Salix herbacea</i> (1), <i>Empetrum nigrum</i> (1), <i>Betula nana</i> (1)	8.8	102.8	7.1	63.5
Padjelanta PADJ (67.31, 16.69)	Sweden	Aug 2–3	580–641	Erect-shrub (S2)	5	<i>Betula nana</i> (5), <i>Empetrum nigrum</i> (5), <i>V. vitis-idaea</i> (3), <i>V. uliginosum</i> (2)	9.5	106.4	7.8	85.3
Val Bercla VALBER (46.47, 9.58)	Switzerland	July 9	2490	Alpine tundra ^a	5	<i>Primula integrifolia</i> (5), <i>Kalmia procumbens</i> (5), <i>Helictotrocha versicolor</i> (5)	8.9	229.0	12.1	104.4

Table 1 (continued)

Study site	Region	Sampling date(s)	Elevation (m a.s.l.)	Habitat type	Number of plots	Focal Species (number of plots present)	Mean July temperature (1990–2015) (°C)	Mean July precipitation (1990–2015) (mm)	Mean July temperature (2015) (°C)	July precipitation (2015) (mm)
Barrow BARR (71.30, –156.67)	USA	Aug 7–8	10	Wetlands (W1)	5	<i>Salix rotundifolia</i> (2), <i>Arctagrostis latifolia</i> (3), <i>Carex aquatilis</i> (5), <i>Salix pulchra</i> (3), <i>Petasites frigidus</i> (1), <i>V. vitis-idea</i> (1)	5.3	21.8	5.1	5.8
Toolik Lake TOOL (68.64, 149.57)	USA	Aug 1	730–746	Graminoid (G4)	5	<i>Betula nana</i> (5), <i>Rhododendron tomentosum</i> (5), <i>V. vitis-idea</i> (5), <i>Eriophorum vaginatum</i> (5), <i>Carex bigelowii</i> (5)	11.6	45.0	11.4	38.6

Sites with 2015 temperatures that differ by more than ± 1 °C from the long-term average are in bold, similarly sites that have 2015 precipitation levels that differ from the long-term mean by more than ± 10 mm are also in bold. Sites are listed geographically.

^aVirtanen et al. (2016)

Table 2 List of all 42 focal vascular plant species, their growth form, total number of sites and plots they were found in, number of samples, total number of leaves analyzed for each species, number of leaves with external damage, gall damage, and mining damage, and the corresponding average percent leaf area damaged (PLAD) for those samples

Focal species	Growth form	Study sites	Plots	Samples	Leaves	External damage	Gall damage	Mine damage	Total damaged	Average PLAD (%)
<i>Betula nana</i> L.	Deciduous shrub	10	45	135	14,779	2176	12	15	2176	2.08
<i>Salix arctica</i> Pall	Deciduous shrub	3	11	23	2299	843	63	9	899	3.18
<i>Salix herbacea</i> L.	Deciduous shrub	3	11	33	3400	1007	3	10	1020	3.89
<i>Salix polaris</i> Wahlenb	Deciduous shrub	3	11	33	3330	40	34	5	79	0.11
<i>Salix pulchra</i> Cham	Deciduous shrub	1	3	3	293	8	2	0	10	0.03
<i>Salix reticulata</i> L.	Deciduous shrub	1	1	3	301	168	9	110	231	9.13
<i>Salix rotundifolia</i> Trautv	Deciduous shrub	1	2	2	200	17	0	0	17	1.29
<i>Vaccinium myrtillus</i> L.	Deciduous shrub	2	9	27	2756	1334	13	59	1384	26.05
<i>Vaccinium uliginosum</i> L.	Deciduous shrub	3	6	18	1883	75	8	8	91	1.08
<i>Andromeda polifolia</i> L.	Evergreen shrub	1	4	12	1203	28	40	0	67	0.30
<i>Calluna vulgaris</i> (L.) Hull	Evergreen shrub	1	5	15	1500	1	0	0	1	0.01
<i>Cassiope tetragona</i> (L.) D. Don	Evergreen shrub	1	4	4	400	0	0	0	0	0
<i>Dryas octopetala</i> L.	Evergreen shrub	2	8	23	2308	212	3	3	216	0.78
<i>Empetrum nigrum</i> L.	Evergreen shrub	7	31	93	9368	70	1	0	71	0.16
<i>Kalmia procumbens</i> (L.) Gift, Kron & P.F. Stevens ex Galasso, Banfi & F. Conti	Evergreen shrub	1	5	5	500	9	13	0	22	0.25
<i>Rhododendron tomentosum</i> Harmaja	Evergreen shrub	1	5	15	1502	3	1	1	5	0.03
<i>Vaccinium vitis-idaea</i> L.	Evergreen shrub	6	25	69	6935	408	720	66	1181	1.46
<i>Arctagrostis latifolia</i> (R. Br.) Griseb	Graminoid	2	7	7	692	6	1	0	7	0.01
<i>Avenella flexuosa</i> (L.) Drejer	Graminoid	1	3	9	947	0	0	0	0	0
<i>Carex aquatilis</i> Wahlenb	Graminoid	2	9	17	1666	33	0	57	90	0.11
<i>Carex bigelowii</i> Torr	Graminoid	2	10	30	2955	191	0	21	211	0.76
<i>Carex</i> spp. L.	Graminoid	1	5	15	1471	143	0	283	407	0.93
<i>Eriophorum vaginatum</i> L.	Graminoid	1	5	15	1471	10	0	7	17	0.03
<i>Festuca rubra</i> L.	Graminoid	1	5	15	1510	1	0	0	1	0
<i>Helictochloa versicolor</i> (Vill.) Romero Zarco	Graminoid	1	5	5	500	1	0	2	3	0.11
<i>Juncus trifidus</i> L.	Graminoid	1	2	6	600	0	0	0	0	0
<i>Luzula confusa</i> Lindeberg	Graminoid	1	3	9	904	74	0	0	74	1.65
<i>Luzula spicata</i> (L.) DC	Graminoid	1	1	3	304	3	0	0	3	0.03
<i>Poa arctica</i> R. Br	Graminoid	1	1	3	300	0	0	0	0	0
<i>Trichophorum cespitosum</i> (L.) Hartm	Graminoid	1	5	12	1175	0	0	0	0	0
<i>Armeria maritima</i> (Mill.) Willd	Herb	2	6	18	1802	145	16	0	161	0.90
<i>Bistorta vivipara</i> (L.) Delarbre	Herb	1	1	3	195	10	0	1	11	0.33

Table 2 (continued)

Focal species	Growth form	Study sites	Plots	Samples	Leaves	External damage	Gall damage	Mine damage	Total damaged	Average PLAD (%)
<i>Cerastium alpinum</i> L.	Herb	1	1	3	299	4	0	7	11	1.57
<i>Cerastium arcticum</i> Lange	Herb	1	2	6	604	15	7	1	23	0.27
<i>Cochlearia groenlandica</i> L.	Herb	1	1	3	300	3	14	0	16	0.54
<i>Oxyria digyna</i> (L.) Hill	Herb	2	3	7	690	65	51	95	199	6.13
<i>Papaver radiculatum</i> Rottb	Herb	1	1	1	97	0	0	10	10	0.73
<i>Petasites frigidus</i> (L.) Fr. s.l	Herb	1	1	1	104	57	0	0	57	1.60
<i>Primula integrifolia</i> L.	Herb	1	5	5	437	35	0	2	37	1.36
<i>Saxifraga hyperborea</i> R. Br	Herb	1	1	3	303	5	1	0	6	0.18
<i>Saxifraga oppositifolia</i> L.	Herb	2	6	17	1701	0	0	0	0	0
<i>Silene acaulis</i> (L.) Jacq	Herb	3	12	36	3602	65	13	0	78	0.36

Some leaves experienced more than one type of herbivory and therefore the total number of leaves damaged is less than the sum of the three damage types in some plant species. In total, 77,586 leaves were examined. Species taxonomy follows Roskov et al. (2017)

Sampling protocol

Three individual plants for each of the focal species at each plot were identified. Plants were considered different “individuals” when they were at least 10 m apart. Leaf samples (ca. 100 leaves per plant individual) were collected from each individual. In the case of plants that did not have enough leaves, samples were collected from “aggregates”, i.e., multiple stems growing close together (within 1–2 m). The selection of individuals or aggregates was undertaken from a distance of 5–10 m to avoid recognition of invertebrate herbivory during the selection process and avoid confirmation bias (i.e., picking individuals specifically because they were damaged or undamaged; Kozlov et al. 2014). In many cases, branches or stems were collected to avoid damaging leaves by detaching them in the field, or missing leaves with a large amount of damage (i.e., only the petiole remaining). Samples were press-dried as herbarium specimens and sent for analysis by the first author.

The contribution of each of the focal species to the biomass in each plot was estimated using the point-intercept method. In each plot, 16 sampling points were placed in a regular grid 5 m apart. Point-intercept data were collected at each sampling point using a 50×50 cm frame with ten fixed pin positions. The number of times a focal species touched each pin was recorded (i.e., multiple hits per pin per focal species were possible). Three of the sampling points were randomly selected to harvest total aboveground plant biomass using the same frame, after the point-intercept data were collected. Biomass samples were stored in paper bags and air-dried in the field; in the lab, biomass samples were sorted into the three focal species recorded for each plot and ‘other’ biomass, and weighed to the nearest mg.

The sampling points that had both point-intercept and biomass data were used to calculate a conversion factor to estimate plant biomass based on point-intercept data as described by Bråthen and Hagberg (2004; Online Resource 2). Biomass estimates for each focal species in each plot were then calculated based on the 16 sampling points, multiplying the mean number of hits per pin of each of the focal species by the corresponding conversion factor.

Leaf damage assessment

Leaf sample preparation involved detaching the leaves from the branches/stems or, for graminoids, at the ligule. All leaves were sampled starting from the uppermost one on each branch/stem, until the desired number of leaves was obtained. A dissecting microscope was used to observe leaves for damage. Each leaf was examined on both sides with a light source shining down on to the leaf to assess external damage, and then, both sides were examined with a light source shining up through the leaf to evaluate internal

damage (Barrio et al. 2017). Leaf mine damage was identified by the presence of invertebrates inside the mines, while galls that were unclear were reviewed by entomologists at the University of Alberta.

The percent area of each leaf that was damaged by invertebrates (either chewing or skeletonization caused by external feeders, mining, or gall damage) was visually attributed to one of the following damage categories: intact leaves, < 1%, 1–5%, 5–25%, 25–50%, 50–75%, and > 75% of leaf area damaged or removed by herbivores (Kozlov 2008; Barrio et al. 2017). When two different types of invertebrate herbivory were present on the same leaf (3.3% of leaves), the second damage type (smaller percentage) was recorded as secondary damage and included in the analysis (see below), but the leaf was not counted twice in the total number of leaves. Data for the damage assessment of *Betula nana* was previously used in Barrio et al. (2017) which focused on examining variation in invertebrate herbivory for a single species complex across the Arctic.

Calculation of community-weighted estimates of biomass lost (CWBL)

As an approximation of foliar loss to invertebrate herbivores, the percent leaf area damaged (PLAD) was calculated as the mean leaf area damaged for each of the focal species in a plot. The number of leaves in each damage category was multiplied by the median value of damage in that category (for example, a leaf in the 25–50% bin was assigned as having 37.5% damage), summed over all damage categories and divided by the total number of leaves in the sample (Barrio et al. 2017).

The community-weighted biomass lost (CWBL, %) due to total invertebrate leaf damage was calculated for each plot (Online Resource 3), taking into account the proportion of biomass contributed by each of the focal species, and how much of this was consumed by invertebrates, as estimated by PLAD. CWBL takes into account the effect of different species composition at different study sites, and allows for comparisons across sites with different habitat types. In order to control for the biomass of the focal species being only a proportion of the total community biomass, the percent contribution of each focal species to the total biomass was incorporated into the CWBL calculation. In the case of Toolik Lake, no total biomass harvest data was available but five focal species were reported; it was assumed that these five focal species represented most of the biomass at the community level and the contribution of each focal species to the biomass of these five focal species was included in the CWBL calculations (Online Resource 3). CWBL was expressed as a percentage of the total biomass in a plot to control for the variation in biomass across tundra sites, from polar deserts to shrub tundra.

Statistical analyses

The combined leaf damage caused by different feeding guilds of invertebrate herbivores (defoliators, miners and gallers) was used in our analysis because some types of leaf damage, such as mining or galling, tend to be infrequent in tundra (Barrio et al. 2017). The variation in CWBL was analyzed using Linear Mixed Effects Models (LMM) (Zuur et al. 2009), including study site as a random factor to account for the study design of multiple plots sampled within each site. Predictor variables included climatic variables (long-term mean July temperature and precipitation, and July 2015 temperature and precipitation relative to the long-term average), total plant biomass per m², and the habitat type of the study site (Table 1; Online Resource 3). Temperature and precipitation data were compiled from the CRU TS3.10 Dataset (Harris et al. 2014), and divided into long-term July means (based on data from 1990–2015) and the deviations from the respective means in July 2015. Long-term means incorporated interannual variation in temperature and precipitation, while the 2015 values indicated deviations in the weather conditions during the sampling year relative to the long-term average (i.e., if the summer 2015 was colder and/or wetter than average at a particular site). July was used to indicate mid-summer conditions that coincide with peak temperatures and peak plant biomass (Myers-Smith et al. 2015; Barrio et al. 2017). The six different habitats included wetlands, erect-shrub tundra, prostrate-shrub tundra, barren tundra, graminoid tundra, and alpine tundra (Table 1).

Five models were constructed (Table 3) based on our a priori hypotheses that herbivory would be driven by: (1) the long-term mean July temperature; or by more additional variables: (2) the long-term mean precipitation, (3) the 2015 deviations from average temperature and precipitation, (4) aboveground plant biomass, or (5) habitat type. The five models were compared using AICc values (Table 3). Collinearity between the predictors was assessed across the 20 sites, and only combinations of variables with correlations $r < |0.55|$ were included in the models (Table 3). Running the analyses with and without the alpine site and with and without Murmansk, which showed the largest value of CWBL (Fig. 2) did not change the results, so these sites were retained in the analyses.

In a separate analysis, we examined whether different plant growth forms and/or functional groups experienced different levels of invertebrate herbivory. Using a Welch's two-sample *t* test, we compared woody plants to herbaceous plants, deciduous shrubs to evergreen shrubs, and herbs to graminoids.

Model assumptions were checked by visually examining plots of the residuals versus fitted values to determine homoscedasticity of variances; normality of residuals was

Fig. 2 The relationship between the mean community-weighted biomass lost (CWBL) to invertebrate herbivores and the mean long-term July temperature. Each point represents a study site ($n=20$); site names are indicated with abbreviations (see Table 1). The fitted line and 95% confidence interval (shaded) are shown. The point with the highest CWBL corresponds to Murmansk (MURM); running the analyses with and without this point did not change the overall trend

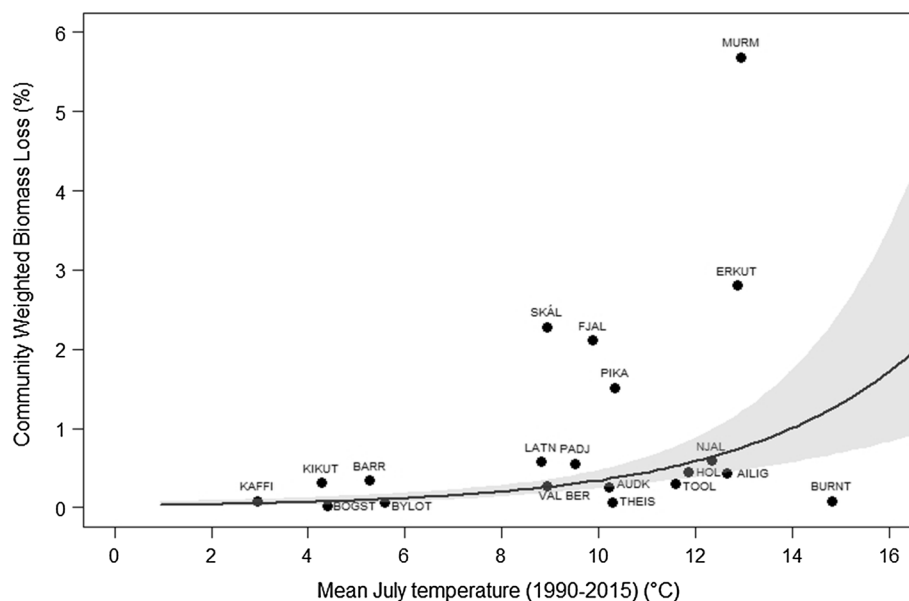


Table 3 The five models used to explain the variation in community-weighted biomass lost (CWBL) to invertebrate herbivory and the null model

Model	Predictors	df	AICc	AICc Weight
Null	N/A	3	142.3	0.06
1	LTMT	4	138.5	0.38
2	LTMT + LTMP	5	140.8	0.13
3	LTMT + DT2015 + DP2015	6	140.8	0.13
4	LTMT + TBM	5	139.6	0.23
5	LTMT + Habitat	9	141.5	0.09

Models were created using Linear Mixed Effects Models with site as a random effect. AICc values and weights are presented for comparison between models

LTMT long-term mean temperature, *LTMP* long-term mean precipitation, *DT2015* 2015 temperature difference, *DP2015* 2015 precipitation difference, *TBM* total plant biomass, *Habitat* site habitat type

examined via QQ-plots. In order to meet the assumptions the CWBL values were $\log_{10}$ -transformed prior to analysis. All statistical analyses were carried out in R 3.5.1 (R Development Core Team 2017), and LMMs were built using the *lme4* package (Bates et al. 2015).

Results

Distribution of damage among herbivore feeding guilds

Invertebrate damage was found in 9062 of 77,586 leaves examined (11.7%). The majority of damaged leaves (7265 or 80.2%) had feeding marks of externally defoliating

invertebrates. We found only 772 mined leaves and 1025 leaves with insect or mite galls (8.5% and 11.3% of all damaged leaves, respectively). Damage by defoliators was recorded in leaves of 35 of the 42 focal plant species, by leaf miners in 21 species, and by gall-forming herbivores in 21 species (Table 2).

Variation in herbivory among focal species

The 42 focal species included in our analyses experienced varying levels of invertebrate herbivory. The highest average percent leaf area damaged (PLAD) from all samples combined was 26.05% (*Vaccinium myrtillus*), while seven plant species had no invertebrate damage at all (Table 2). Only 13 species experienced leaf area losses greater than 1%, with only three of those species experiencing more than 5% (*V. myrtillus*, *Salix reticulata* (9.13%), and *Oxyria digyna* (6.13%); Table 2).

We found differences in invertebrate herbivory between plant growth forms and/or functional groups. Foliar losses of woody plants were four times higher than that of herbaceous plants (2.93% vs. 0.70%; $t_{561.42} = 5.16$, $p < 0.0001$). Within woody plants, the losses of deciduous shrubs were 14 times greater than the losses of evergreen shrubs (5.20% vs. 0.37%; $t_{285.17} = 5.38$, $p < 0.0001$). Within herbaceous plants, the losses of herbs were four times as large as the losses of graminoids (1.16% vs. 0.28%; $t_{121.15} = 2.50$, $p = 0.0137$).

Variation in herbivory among study sites

At the site level, the CWBL due to invertebrate herbivores varied from 0.02% (Bogstranda, in Svalbard) to 5.68% (Murmansk, Russia), with an average ($\pm$ SE) of $0.94 \pm 0.31\%$

($n=20$; Fig. 1; Online Resource 3). Aboveground biomass of vascular plants at our plots ranged from 2.56 to 854.68 g/m². CWBL ranged between 0.002 and 10.68% across all plots examined, with an average ($\pm$ SE) of $0.98 \pm 0.17\%$ ($n=92$).

Two models received similar support ($\Delta AIC_c < 2$; models 1 and 4 in Table 3). Both models included the effect of long-term mean July temperature (Table 3); the second best model also included total aboveground biomass, but its effect was not significantly different from zero (*estimate* = -0.001 , 95% CI = $(-0.002, 0)$; Online Resource 4). The models predicted a linear positive relationship between the log-transformed community-weighted biomass lost (CWBL) and July temperature (Fig. 2), with an estimated increase of 0.11% CWBL per 1 °C (model 1: *estimate* = 0.106, 95% CI = $(0.028, 0.184)$; [model 4: *estimate* = 0.114, 95% CI = $(0.038, 0.190)$]. However, the models still had a high percentage of unexplained variability between the different tundra sites, associated with the random effect (model 1: 67.73%, model 4: 65.14%; Online Resource 4).

Discussion

Invertebrate herbivory was detected at all our 20 study sites, suggesting that it is a widespread phenomenon throughout the tundra biome. However, the intensity of herbivory was generally low and seemed to be influenced by summer temperature and other unknown local site characteristics.

At the community level, the mean foliar biomass lost to invertebrates was 0.94% ($n=20$), ranging from 0.02 to 5.69%. These levels are consistent with the average value of 0.56% reported from shrubs growing in tundra regions of the European Arctic (Kozlov et al. 2015a) and with an estimate of 1.20% loss calculated from the regressions of woody plant herbivory vs. latitude (after Kozlov et al. 2015b) for the average latitude of our Arctic study sites (68.1°N). Thus, we conclude that in tundra, plant foliar losses to invertebrate herbivores at background (i.e., non-outbreak) levels are around 1% of foliar biomass. This value is 5–13 times lower than reported in temperate plant communities. For example, in temperate herbaceous communities, invertebrates reduced plant biomass by 13% (Coupe and Cahill 2003), and tissue loss due to invertebrates in temperate forests was 5–8% (Kozlov et al. 2015b). This discrepancy may be partially attributed to the species-specific data used for the temperate studies compared to the community-weighted method used in our study, or may simply reflect the lower levels of invertebrate herbivory in the tundra (Kozlov et al. 2015a).

The variation in community-weighted biomass lost to background invertebrate herbivory was associated with long-term summer temperatures. Our sites spanned a range of summer (July) temperatures across the tundra biome,

from 2.9 to 14.8 °C. Warmer sites had significantly higher levels of invertebrate herbivory despite a large variation among sites. Our model indicated a logarithmic relationship between long-term July temperature and CWBL, suggesting that sites with higher temperatures have a more pronounced increase in herbivory than cooler sites. As a first step to approximate the effects of future warming on tundra invertebrate herbivory, we can adopt a space-for-time substitution approach to broadly infer changes in herbivory from locations with different climatic variables (see for example Barrio et al. 2017). Given the lack of long-term monitoring data on invertebrate herbivory in tundra and despite its limitations, this approach provides the best solution and allows generating predictions that can then be tested through monitoring or manipulative field experiments. According to our model, a single degree increase in temperature will have a stronger effect on herbivory levels at higher temperatures (i.e., in the low Arctic) compared with lower temperatures (i.e., in the high Arctic). For example, an increase in temperature from 4 to 5 °C results in an increase in CWBL of 0.02%, while increasing from 13 to 14 °C results in an increase of 0.20%. Depending on the scenario, global temperatures are predicted to increase by 1.1–2.9 °C to 2.4–6.4 °C over the next century, and this increase is expected to be more pronounced in the Arctic (IPCC 2013; Overland et al. 2017). These predicted increases in temperature would shift even our coldest sites (in Svalbard, Norway; 2.9 °C) into the temperature range where herbivory levels begin to increase more rapidly (Fig. 2). We also found that for sites with mean temperatures < 6 °C, there was very little variation in herbivory level – it was always very low and all observations were clustered near the trend line. However, at sites with mean July temperatures > 8 °C, the intensity of herbivory becomes much more variable, with some sites showing low herbivory while others had much higher levels. This suggests that a threshold may exist, below which invertebrate herbivory is consistently low. Once this threshold is crossed at higher temperatures, herbivory can sometimes be very high but other site-specific factor(s) may be constraining the levels of herbivory, resulting in the variability observed in the present study (Fig. 2). However, our assessment was based on a single year and temporal variation may not be consistent across sites, highlighting the need for long-term monitoring of invertebrate herbivory across multiple sites in tundra ecosystems.

Our models indicate that long-term mid-summer temperatures are partially responsible for this trend rather than the climatic conditions in the year of sampling. This may be partially related to the life histories of high-latitude insects, which tend to have life cycles that span multiple years (Danks 1992). Warmer summers year after year may thus have a greater effect than one single warm season, if, for example, insects are able to complete their life cycle in

fewer growing seasons, or if species are able to complete multiple generations in a single summer. Further, long-term warming could allow lower-latitude species (with shorter generation times, higher growth rates, and warmer temperature requirements) to persist at higher latitudes. In contrast, other studies have found that weather in the year of sampling has a stronger effect on herbivory than long-term climate data (Kozlov et al. 2013; Barrio et al. 2017). These studies however, were investigating herbivory levels on a single or a few plant species rather than at the community level. The number of plant species involved in studies estimating herbivore damage can affect the inferences of these studies, with studies including fewer species tending to overestimate damage (Zvereva and Kozlov 2019). Warming can also influence the feeding choices of invertebrate herbivores (Barrio et al. 2016a; Gamarra et al. 2018), so patterns of herbivory of a single species may not be representative of what happens at the community level. An alternative explanation could be simply that the weather in the year of sampling in the present study might have been unusual. Most sites had a colder (14 out of 20) and drier (16 out of 20) summer than their long-term average. Longer-term monitoring may be able to capture the effects of interannual temperature variation on herbivory, and this could be effectively implemented through coordinated efforts like the Circumpolar Biodiversity Monitoring Programme (CBMP; e.g., Gillespie et al. 2019).

Our models including precipitation had little support in explaining the variation in background invertebrate herbivory (Table 3), but this does not rule out an important role for precipitation as a mediating factor in changing tundra environments (Bintanja and Andry 2017). Barrio et al. (2017) found a positive effect of both temperature and precipitation when examining herbivory on dwarf birch (*B. glandulosa-nana*) across the tundra biome. Again, this could be an indication that patterns at the species level may not hold at the community level. Precipitation can influence invertebrate herbivory through its effects on leaf toughness, yet at the community level this effect could be masked because the community can be made up of plant species with varying levels of drought tolerance.

A large percentage of the variation in invertebrate herbivory however was not explained by the effect of long-term mean summer temperature (i.e., the variance associated with the random effect of site was 67.73%). This suggests that local site characteristics other than temperature are driving differences in herbivory between the sites, and emphasizes the usefulness of longitudinal studies, such as the present one, to better explore the role of climate on biotic interactions at a biome-wide scale. This site-specificity is consistent with recent studies that have found strong local effects in the structuring of Arctic arthropod communities (Hansen et al. 2016). For example, local variation in shrub cover can influence the composition of the arthropod community

assemblage, through locally increasing habitat structural complexity, such that higher shrub cover leads to a larger and more diverse community of arthropods (Rich et al. 2013; Asmus et al. 2018). At a local scale, herbivory rates can also be influenced by nutrient concentrations in the soil that influence leaf quality (Semenchuk et al. 2015). Higher nutrient concentrations can lead to increased palatability of plant species, and ultimately higher levels of herbivory (Torp et al. 2010a, b; Semenchuk et al. 2015). Presence of vertebrate herbivores may also affect the intensity of invertebrate herbivory through their direct and indirect effects on the abundance of invertebrate herbivores (Suominen et al. 1999, 2003).

Other local drivers, such as snow cover, can also contribute to small-scale heterogeneity in tundra landscapes (Kankaanpää et al. 2018). Snow cover can vary substantially on a local scale due to variations in topography (e.g., hollows with deep snow vs. windswept areas with little snow) (Torp et al. 2010a, b). Variation in the duration of snow cover can influence overwinter protection of plants (Torp et al. 2010a) and invertebrates (Danks 2004), timing of emergence for plants (Torp et al. 2010a) and invertebrates (Høye and Forchhammer 2008), the level of nitrogen in the soil (Semenchuk et al. 2015) and subsequently in leaf tissue (Torp et al. 2010a, b; Semenchuk et al. 2015), as well as the local composition of arthropod communities in tundra (Kankaanpää et al. 2018). Accounting for the variation in these local drivers and their effects on invertebrate herbivory would require site-specific measurements, but represent a critical step to understand the variability in the observed patterns of herbivory.

Lastly, the structure and composition of plant communities may also influence invertebrate herbivory. In general, different growth forms have differing leaf tissue palatability such that deciduous plants are more palatable than evergreens (MacLean Jr. and Jensen 1985; Turcotte et al. 2014). Within this study, the 13 species that had > 1% of their leaf area lost were deciduous shrubs (7 species), herbaceous species (4), graminoids (1), and one palatable evergreen shrub (*Vaccinium vitis-idaea*). As well, deciduous shrubs had an average of 5.20% of their leaf area consumed compared with 1.16% for herbs, 0.37% for evergreen shrubs, and 0.28% for graminoids. This result supports our hypothesis that different plant functional groups experience different levels of herbivory, with more palatable groups experiencing more damage. These differences in the palatability of growth forms can translate into the differences observed between sites. For example, we measured the highest levels of background herbivory in Murmansk, where a large proportion (49.5%) of the focal species biomass corresponded to *V. myrtillus* and *B. nana*, both of which are palatable deciduous shrubs (MacLean Jr. and Jensen 1985). In contrast, Theistareykir in Iceland had one of the lowest levels of herbivory (0.06%)

and two of the three focal species at this site were unpalatable evergreen shrubs (*Empetrum nigrum* and *Calluna vulgaris*). In the long term, shifts in plant community composition due to climate change—if more palatable plant species are favored—could amplify the effects of warming on insect herbivory predicted by our model. In this sense, assessing herbivory at the plant community level, while masking some of the individual species-specific responses, may be more representative of a more diverse invertebrate herbivore community, and ultimately of ecosystem responses to environmental changes.

Conclusions

Our study provides a first assessment of herbivory at the community level across the tundra biome, providing a valuable baseline reference for evaluating future changes. Background invertebrate herbivory in the tundra biome at the community level is low (the average loss of foliar biomass is 0.94%). Our study suggests that plant losses to invertebrate herbivores in the tundra biome should increase, at least at some sites, as the climate warms, even if some of these losses could be offset by increased plant biomass production under warming (Day et al. 2008). Clarifying to what degree the relationship between climate and invertebrate herbivory is a direct effect of warmer temperature, or an indirect effect of warming temperatures on plant phenology, physiology, or abundance will help predict how the level of invertebrate herbivory on tundra plants will change in response to a warmer climate. Our results also emphasize that most of the variation in background invertebrate herbivory is associated with local site characteristics and highlights knowledge gaps in our understanding of invertebrate herbivory in tundra. It is important, however, to keep in mind that our results represent a single-year snapshot: future studies should include observations over longer periods of time to estimate year-to-year variation in the intensity of herbivory, as temporal variation is also likely to play an important role. Ideally, future research should also include characterizations of the invertebrate herbivore communities and their changes over time.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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